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“Coastal” versus “inland” shorebird species: interlinked fundamental dichotomies between their life- and demographic histories?

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In this contribution I present an extended but testable hypothesis (or “evolutionary scenario”) to explain how and why many life-history features of latitudinal migrant shorebirds, basically characterised by the correlation between habitat choice in the winter and the breeding season, may be functionally and causally intertwined. The most novel (and contentious) aspect of the hypothesis is that historical restrictions in suitable habitat may generate further restriction of suitable habitat with the causal chain consisting of population bottlenecks, leading to reduced adaptive genetic variation, leading to reduced ability to fight diseases, thus affecting potential habitat choice.

INTRODUCTION

The life-histories of the 86 sandpiper species (Scolopacidae), 66 plovers (Charadriidae), 11 oystercatchers (Haematopodidae) and 7 stilts (Recurvirostridae) encompass a vast spectrum of migration strategies, habitat selection, foraging styles, degrees of plumage polymorphism and mating systems (see respectively Piersma *et al.* 1996, Piersma & Wiersma 1996, Hockey 1996, Pierce 1996). Yet, these birds also share many basic biological features: low reproductive rates with a clutch of 3 or 4 eggs, open nests, precocial chicks (Schekkerman *et al.* 2003), reliance on wetland ecosystems, relatively high Basal Metabolic Rates (Kersten & Piersma 1994) and relatively long lives (Goede 1993). As shown below, within the long-distance (latitudinal) migrant species of the sandpiper and plover families, covariation in life-history strategies can be detected, involving population size, extent and predictability of selected habitats, and migration distances. This cline in life history strategies is characterised by the correlation between habitat choice in winter and in the breeding season.

THE PATTERNS

Shorebird species breeding in the High Arctic usually spend the winter in marine habitats, whereas species breeding south of the tundra desert belt tend to winter in more freshwater habitats (Piersma 1997). Note (1) that freshwater habitats include lowland and upland grasslands used e.g. by tundra plovers *Pluvialis* during the nonbreeding season and by curlew species *Numenius* and Upland Sandpipers *Barramia longicauda* throughout the year and (2) that saline inland habitats may well qualify (at least in terms of disease organisms) as “marine” habitats.

Indeed, when the breeding and the wintering habitats of the 24 different species of the sandpiper subfamily Calidrinae are ranked as “decreasingly high arctic and alpine” and “de-

creasingly marine/saline”, the covariation is clearly shown (Fig. 1). There are exceptions to the rule such as Buff-breasted Sandpipers *Tryngites subruficollis* (number 23 in Fig. 1) breeding in the High Arctic and wintering at inland pasture sites in Patagonia, but the Spearman rank correlation coefficient is 0.70, a value that is statistically significant from zero ($p < 0.01$). Red Knots *Calidris canutus* and Ruffs *Philomachus pugnax* occupy the extremes, the first being one of the most highly arctic breeders wintering exclusively in coastal marine environments, the second being the southernmost breeding sandpiper species wintering exclusively in inland and freshwater habitats. Of course, there is an element of subjectivity in the ranking of the species’ habitat characteristics. However, as the outlying groups are perfectly clear-cut, the association demonstrated here seems robust.

In addition, shorebirds wintering in marine habitats tend to have smaller population sizes than shorebirds wintering in freshwater habitats (Piersma 1986). The low latitude/freshwater species tend to have shorter overall migration distances, which are covered by a greater number of shorter flights than the high latitude/marine species (Piersma 1997). Although the genetic variability in shorebirds appears to be quite low overall (Baker & Strauch 1988), a comparison of two sandpipers (Dunlin *Calidris alpina* and Red Knot) has established that the northernmost breeding species (the Red Knot) was hit by the severest population bottlenecks in the late Pleistocene and Holocene (Baker & Marshall 1997). Also, allozyme assays of genetic variation seem to show that the Ruff, the southernmost breeding and most inland wintering sandpiper species has much greater variation (Segre *et al.* 1970) than Dunlin and Red Knot (Baker 1992). Indeed, within the genus *Calidris*, a measure of genetic variability, mean heterozygosity as reported by Baker (1992), is positively correlated with the rank order of wintering habitat, i.e. the relative use of freshwater habitats (Fig. 2; note that the correlation with the rank order of breeding habitat is positive but not significant).



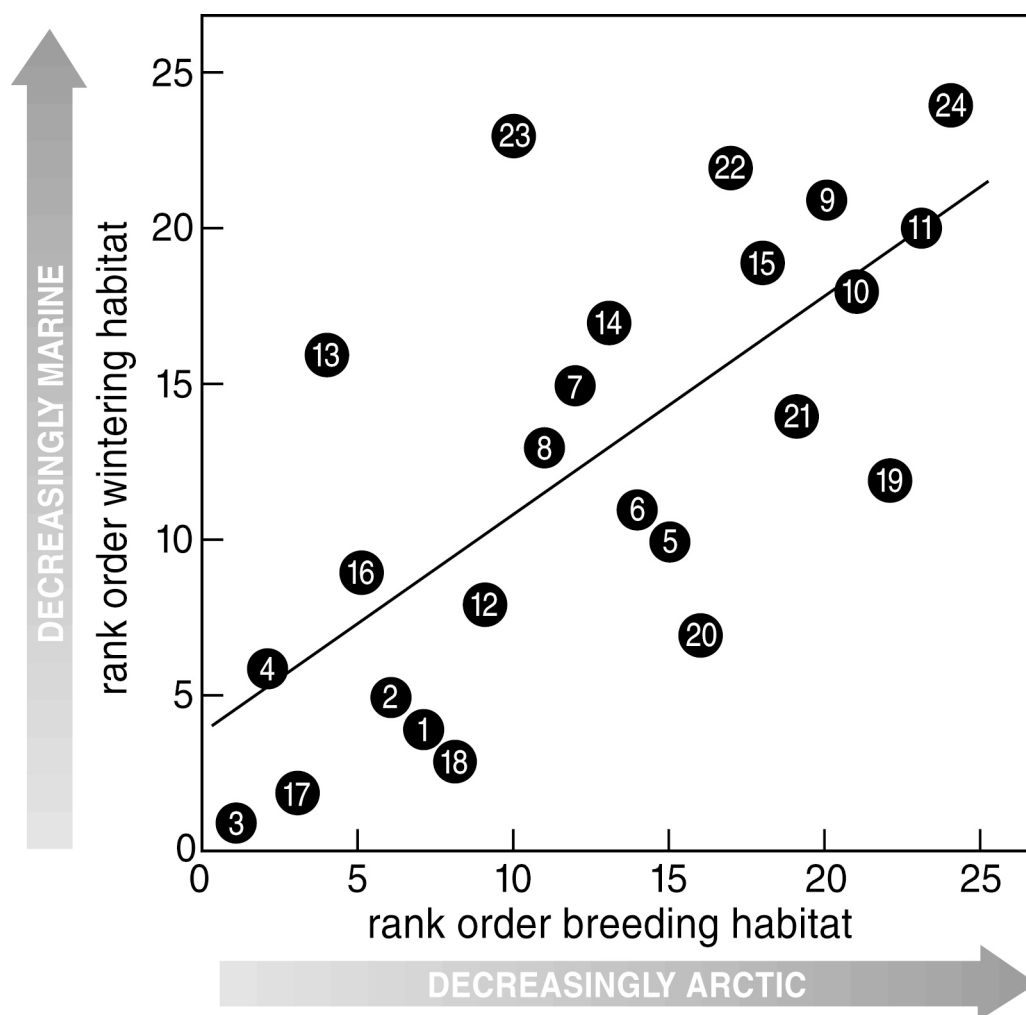


Fig. 1. Correlation between the extent to which shorebird species belonging to the subfamily Calidrinae (Scolopacidae) breed in decreasingly arctic/alpine, open and climatically extreme habitats (rank order breeding habitat) and the extent to which they winter increasingly in fresh-water rather than marine habitats (rank order wintering habitat). The linear regression line is shown to lead the eye. Rank orders compiled from data in Piersma *et al.* (1996) using the midpoint of the breeding ranges to assess the rank number of breeding habitat. 1: *Aphriza virgata*; 2: *Calidris tenuirostris*; 3: *Calidris canutus*; 4: *Calidris alba*; 5: *Calidris pusilla*; 6: *Calidris mauri*; 7: *Calidris ruficollis*; 8: *Calidris minuta*; 9: *Calidris temminckii*; 10: *Calidris subminuta*; 11: *Calidris minutilla*; 12: *Calidris fuscicollis*; 13: *Calidris bairdii*; 14: *Calidris melanotos*; 15: *Calidris acuminata*; 16: *Calidris ferruginea*; 17: *Calidris maritima*; 18: *Calidris ptilocnemis*; 19: *Calidris alpina*; 20: *Eurynorhynchus pygmeus*; 21: *Limicola falcinellus*; 22: *Micropalama himantopus*; 23: *Tryngites subruficollis*; 24: *Philomachus pugnax*.

THE HYPOTHESIS

Based upon arguments developed earlier (Piersma 1997), I suggest that the covariation between breeding latitude and wintering habitat may reflect co-evolved life history complexes along correlated latitudinal (with respect to breeding area) and marine-freshwater habitat (nonbreeding areas) axes. For heuristic purposes, one can take the extremes of the latitude/habitat axes to develop a hypothesis about the evolutionary linkages between demographic bottlenecks, disease and nutritional factors and ecological characteristics (Fig. 3). Although freshwater wetland habitats used by shorebirds are usually ephemeral and unpredictable, low-latitude breeding species using these habitats have large parts of continents to live in. This would explain the relatively large population sizes and the possible paucity of historical population bottlenecks (the latter remains to be established).

In contrast, extreme habitat specialists that breed on high arctic tundra and winter in (coastal) marine habitats are lim-

ited to suitable parts of the continental fringes where intertidal soft sediments or rich rocky shorelines occur. The available area of habitat is one- rather than two-dimensional and thus much smaller than that of inland winterers. This is true not only in winter but also during migration – long flights are necessary to bridge the distances between suitable staging areas. During times of rapid climate change and shrinking habitats, their already small populations would become even further reduced. If severe population bottlenecking continued, serial loss of adaptive genetic variation in the genes coding for the immune system (i.e. genes coding for antigen recognition sites or natural antibodies) could occur (O'Brien & Evermann 1988). The recently population-bottlenecked Red Knot is a case in point (Baker *et al.* 1994, see Avise 2000) and could be called the avian equivalent of the Cheetah *Acinonyx jubatus*. Cheetahs exhibit very low levels of genetic variation, probably because of a severe recent population bottleneck also (Caro 1994). This low genetic variation appears correlated with increased susceptibility to infec-



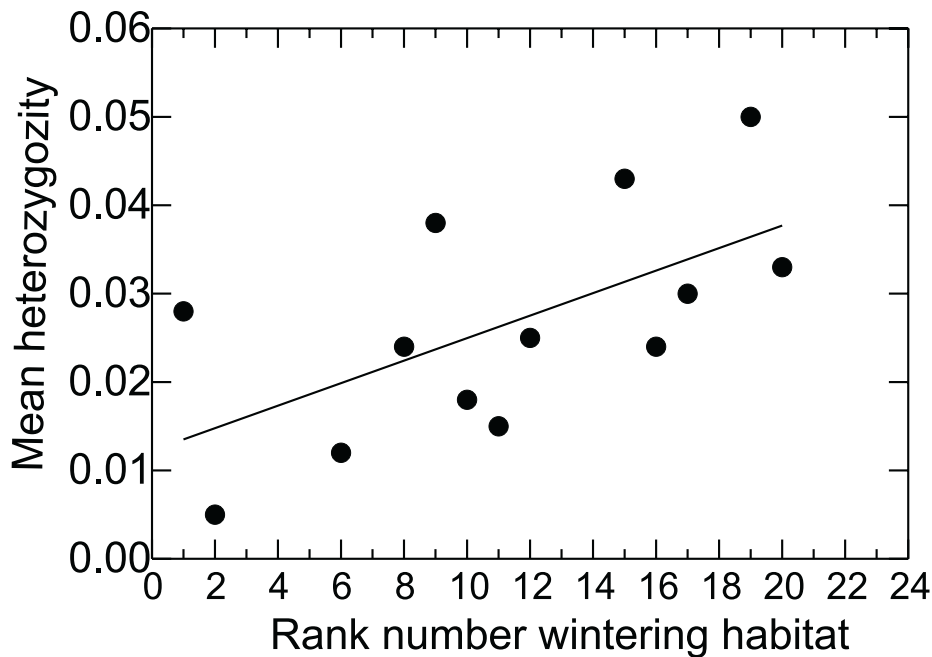


Fig. 2. Relationship between the mean heterozygosity of *Calidris* species (a measure of genetic variability; from Baker 1992: Table 1) and the rank number of the wintering habitat (where the lowest numbers refer to the most marine habitat choice) as the y-axis in Fig. 1 (Spearman rank correlation coefficient is 0.58, $n = 13$, $p < 0.05$). The linear regression line is shown to lead the eye.

tious diseases (O'Brien *et al.* 1985), perhaps caused by reduced variability in the Major Histocompatibility Complex (MHC, the part of the genome that codes for adaptive immunity; see e.g. Zelano & Edwards 2002). Additionally, or alternatively, in high latitude/marine species the *expression* of immunocompetence may be further compromised due to long flights necessitating extreme physical performance and nutritional imbalances (Piersma 1987).

If an increased susceptibility to disease restricted the range of suitable habitats (e.g. birds having to avoid areas with ample food but many [vectors for] debilitating diseases, such as mosquitoes carrying avian malaria), we have a system with a strong positive historical feedback link (Fig. 3). This is rather more exciting than a system where historical ecological constraints have simply led to a loss of genetic variation for disease resistance; that is, lowered disease resistance being just a *consequence* (and not also a cause) of population bottlenecks due to temporary restrictions in habitat availability.

Thus, habitat selection, population size, migration strategies and disease resistance may all be linked to the same historical web of causality. In fact, there are several additional biological contrasts that may be relevant: the more pronounced seasonal plumage dimorphism in the high latitude breeding species (Jukema & Piersma 2000), their greater apparent organ flexibility (Piersma 1998) and the suggestion that freshwater species seem to first migrate northwards from the circa-tropical wintering areas at earlier ages than the coastal species (D.I. Rogers pers. comm.). Also, freshwater species of shorebirds appear to have a lower "lifespan energy potential" (spend less energy per maximum lifetime) than marine species (Goede 1993).

DISCUSSION

What I have outlined here is a hypothesis that connects several life-history observations on latitudinal migrant shorebirds with some mechanistic biological processes. Some parts of the overall hypothesis (or evolutionary scenario) are well established, but bigger parts need filling in. Whatever its truth, the hypothesis should be challenging and stimulating, and encourage a wide range of research activities to be started up and research outcomes to be connected. Although it might not be immediately obvious that the system suggested, or the problems posed, will be amenable to insightful investigation, I strongly believe that careful use of nested hierarchies of tests of competing hypotheses would help us to make rapid progress with this research programme. For example, at the level of interspecific comparisons, impaired immunocompetence in arctic/marine species could result from either serial losses of genetic variation or from reduced expression under nutritional stress or increased exercise. The competing hypotheses can be tested in a series of comparisons of species pairs, where immunocompetence assays would be carried out in exercised vs. unexercised, or well fed vs. nutritionally constrained individuals. Such tests could be carried out for species pairs of other groups of animals that have similar ecological dichotomies. There is a research programme with comparable lines of thinking that is currently underway, comparing the life histories of temperate and tropical passerines in the Americas (R.E. Ricklefs pers. comm.).

Relevant pairwise species comparisons could be made for (1) current population trends and demography, (2) habitat selection, (3) migration strategies, (4) past demographic



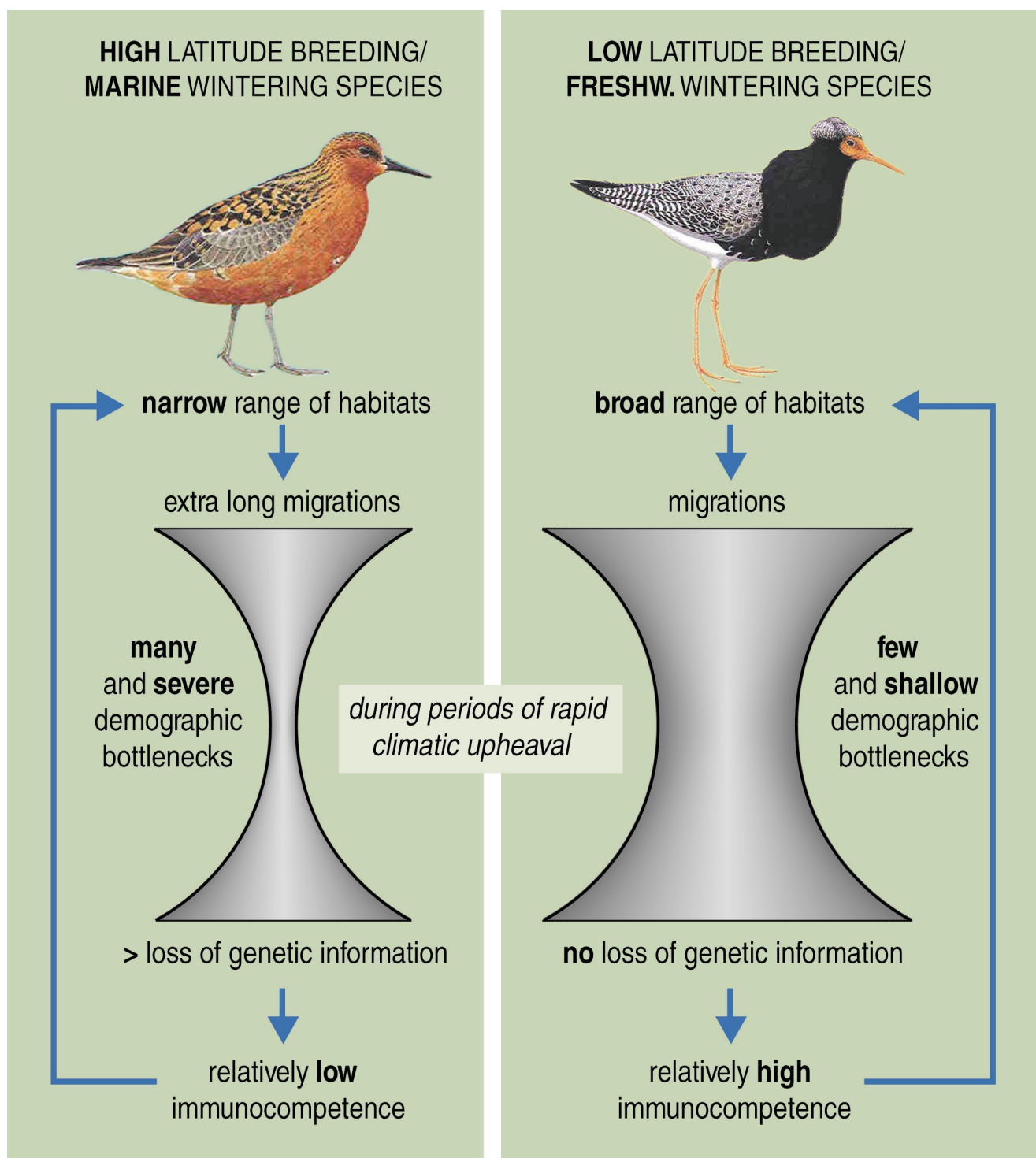


Fig. 3. Schematic overview of the contrasts between latitudinal migrant shorebird species that breed at high latitudes and spend the winter in marine (saline) habitats and those that breed at lower latitudes and spend the winter in freshwater (including grassland) habitats and the possible consequences and positive feedbacks induced by population bottlenecks.



bottlenecks, (5) MHC variation and (6) various aspects of immunocompetence. Based on the latest phylogeny for the 170 species of shorebirds (T. Paton & A.J. Baker in prep.), the following species pairs would be relevant and useful for studies in Western Europe (with the first species denoting the arctic/marine member of the pair): sandpipers (Red Knot vs. Ruff), godwits (Bar-tailed Godwit *Limosa lapponica* vs. Black-tailed Godwit *L. limosa*), tundra plovers (Grey Plover *Pluvialis squatarola* vs. Eurasian Golden Plover *P. aprinaria*) and ringed plovers (Ringed Plover *Charadrius hiaticula* vs. Little Ringed Plover *Ch. dubius*). A similar range of questions can be asked about intra-specific systems. For example, we can use species with a very wide latitudinal breeding range (Dunlin, Ringed Plover and Ruddy Turnstone *Arenaria interpres*), where the northernmost populations usually winter furthest south (leap-frog migration), for paired comparisons between northern and southern populations (or subspecies). Red Knots, that offer six different subspecies with slightly different population histories (D.M. Buehler & A.J. Baker pers. comm.) and a large range in migration distances (Piersma & Davidson 1992), may enable an intraspecific test of the roles of exercise and energy expenditure on disease susceptibility in a bottlenecked species.

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